

# Contemporary life history characteristics of Lake Superior deepwater ciscoes

T. C. Pratt<sup>1,\*</sup> and S. C. Chong<sup>2</sup>

<sup>1</sup>Fisheries and Oceans Canada, 1219 Queen St. East, Sault Ste Marie, Ontario P6A 2E5

<sup>2</sup>Ontario Ministry of Natural Resources, 1235 Queen St. East, Sault Ste Marie, Ontario P6A 2E5

\*Corresponding author: thomas.pratt@dfo-mpo.gc.ca

---

*The diversity and abundance of ciscoes has declined in the Great Lakes, with only Lake Superior retaining its original Cisco fauna; yet as a group, ciscoes remain poorly studied. We examined age and growth, sex ratios, and estimated survivorship and mortality of deepwater ciscoes (Bloater: *Coregonus hoyi*, Kiyi: *C. kiyi*, and Shortjaw Cisco: *C. zenithicus*) and Cisco *C. artedi*. All fish were captured in gill nets set >60 m in Canadian waters of Lake Superior from 2007–2009. Survivorship was higher than expected, with total annual survival rates ranging from 0.615 (Kiyi) to 0.785 (Shortjaw Cisco). This result was attributed to using otoliths to estimate ages rather than scales as done in previous investigations. Maximum ages of ciscoes exceeded 20 years with Cisco, the largest, longest-lived species, followed by Shortjaw Cisco, Bloater and Kiyi. Females dominated adult populations in all species; females were larger-at-age and had greater longevity, resulting in sex ratios skewed heavily towards females. With the exception of age and growth data, the life history characteristics that we observed were consistent with historic data from the early part of the 20th century.*

**Keywords:** mortality, survivorship, sex ratio, female dominance in ciscoes

---

## Introduction

The importance of the loss of Cisco diversity in the North American Laurentian Great Lakes is only now being recognized by Great Lakes fishery managers (Zimmerman and Krueger, 2009). Three of the seven cisco species originally identified from the Great Lakes are extinct, and the remaining communities continue to be greatly diminished (Smith, 1972; Todd and Smith, 1992; Zimmerman and Krueger, 2009). Ciscoes are an important ecological integrator in deep lakes as a trophic connection between offshore benthic invertebrate production and piscine predators, and there is interest in restoring ciscoes to help stabilize and recover deepwater food webs (Favé and Turgeon, 2008; Zimmerman and Krueger, 2009). Lake Superior, with four species,

has the most intact Cisco fauna of any Great Lake. These include Cisco (*Coregonus artedi*), considered a shallow water form, and Bloater (*C. hoyi*), Kiyi (*C. kiyi*), and Shortjaw Cisco (*C. zenithicus*), which collectively make up the deepwater ciscoes.

Recent retrospective analyses have demonstrated tremendous shifts in the composition of the Deepwater Cisco community in Lake Superior since the historic coregonid surveys of Koelz (1929), with Bloater and Cisco nearly completely replacing the formerly dominant Shortjaw Cisco which is at less than 1% of its former abundance (Hoff and Todd, 2004; Gorman and Todd, 2007; Bronte et al., 2010; Gorman, 2012; Pratt, 2012). As a result of extirpations in the other Great Lakes and declining abundance in Lake Superior, both Kiyi (Special Concern) and Shortjaw Cisco (Threatened) are considered

species of conservation concern by the Committee on the Status of Endangered Wildlife in Canada, the independent scientific body that recommends species conservation status to the Government of Canada.

An understanding of the basic ecology, life history characteristics, and population dynamics of Lake Superior ciscoes will help managers to maintain Cisco diversity in Lake Superior, and to potentially re-establish ciscoes in the other Great Lakes. The life history characteristics of the commercially important Cisco has received recent attention (Yule et al., 2008; Stockwell et al., 2009), but the life history characteristics of deepwater ciscoes in Lake Superior has not been updated for many decades (Bloater: Dryer and Beil, 1968; Kiyi: Koelz, 1929; Shortjaw Cisco: Van Oosten, 1937). The use of otoliths, as opposed to the historical use of scales, to interpret the age of Cisco has revealed that Cisco in Lake Superior is much older and has higher survival rates than previously reported (Yule et al., 2008).

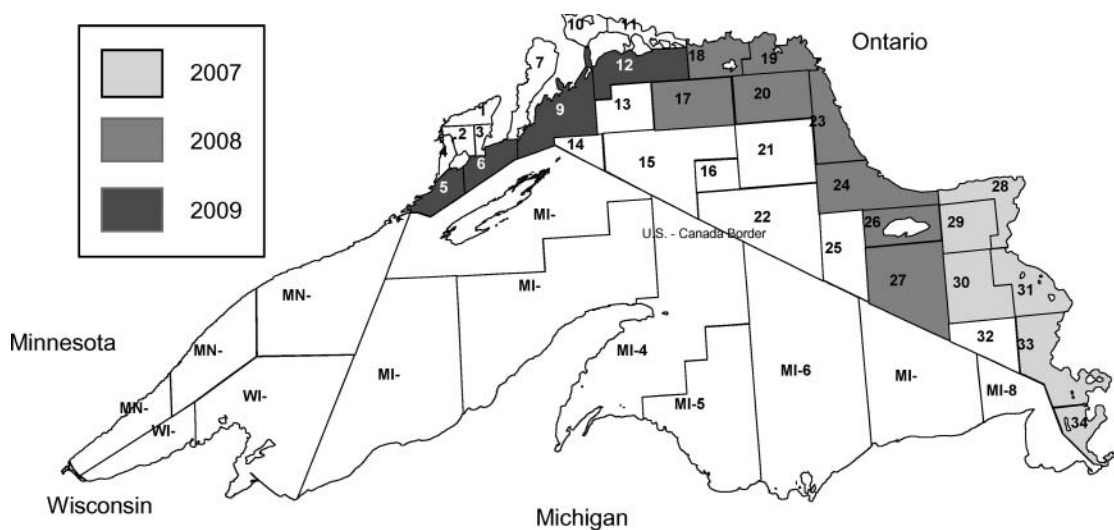
The relative abundance, distribution and habitat associations of deepwater ciscoes in Lake Superior were reported on in Pratt (2012). In this article, we provide basic age, growth, and sex ratio data, and provide estimates of survivorship and mortality, from poorly studied Bloater, Cisco, Kiyi, and Shortjaw Cisco populations from Lake Superior. Where possible, we contrast the observed life history characteristics among species and between sexes. We include data on Cisco, despite its reputation as a shallow-water fish, as it was captured in high abun-

dance even in our deepest gill net sets and is an important component of the Deepwater Cisco community in Lake Superior.

## Methods

A total of 79 experimental gill nets were set deeper than 60 m (mean depth = 109 m, range = 61 to 200 m) in Canadian waters of Lake Superior (Figure 1). The eastern part of the sampling region (management units 28, 29, 30, 31, 33 and 34-16 sets) were fished in 2007, the northern areas (management units 17, 18, 19, 20, 23, 24, 26, and 27-24 sets) were fished in 2008, and western areas (management units 5, 6, 9 and 12-39 sets) were fished in 2009 (Figure 1). The experimental net consisted of eight randomly assigned 46 m monofilament panels, with stretched mesh sizes of 38, 45, 51, 57, 64, 70, 76 and 89 mm. Sampling dates and locations, and the number of nets fished in a given year, are presented in Table 1.

Gill nets were deployed overnight on the bottom (mean soak time 20 h). Gill net catches were tallied on-board by mesh size, and total weight of fish caught in each net was taken for each species. All captured ciscoes were frozen onboard and returned to the laboratory for identification and analyses. In the laboratory, frozen fish were thawed, photographed (full body, head and gill rakers), weighed and total length recorded. Fish were identified by three biologists; identifications were



**Figure 1.** Map displaying the fisheries management zones sampled, by year, from the Deepwater Cisco survey in Lake Superior.

**Table 1.** The sampling location, sampling dates, number of net sets and number of ciscoes captured for each of the three years of Deepwater Cisco sampling in Canadian waters of Lake Superior. See Figure 1 for a description of which management units were sampled in a given year.

| Year | Sampling location      | Sampling dates  | Effort (# nets) | Bloater |             | Cisco |            | Kiyi  |            | Shortjaw Cisco |            |
|------|------------------------|-----------------|-----------------|---------|-------------|-------|------------|-------|------------|----------------|------------|
|      |                        |                 |                 | Total   | Mean (±SE)  | Total | Mean (±SE) | Total | Mean (±SE) | Total          | Mean (±SE) |
| 2007 | Eastern Lake Superior  | 19 June–18 July | 16              | 335     | 20.9 (5.5)  | 136   | 8.5 (1.6)  | 132   | 8.3 (2.5)  | 105            | 6.6 (1.7)  |
| 2008 | Northern Lake Superior | 8 June–7 July   | 24              | 636     | 26.5 (9.2)  | 212   | 8.8 (2.2)  | 135   | 5.6 (1.9)  | 60             | 2.5 (0.8)  |
| 2009 | Western Lake Superior  | 8 June–6 July   | 39              | 2740    | 70.3 (14.5) | 1149  | 29.5 (4.5) | 153   | 3.9 (0.9)  | 223            | 5.7 (0.9)  |
|      |                        | Totals          | 79              | 3711    | 47.0 (8.1)  | 1497  | 19.0 (2.6) | 420   | 5.3 (0.9)  | 388            | 4.9 (0.6)  |

based on a number of unpublished keys. Biological parameters including fork, standard, and total length (mm), weight (g), gender and state of maturity were taken from the majority of specimens, though when catches were high from specific sites only basic parameters (length and weight) were collected once sample sizes were >200 fish. Gill rakers were removed from processed fish and stored in 70% ethanol.

Pairs of sagittal otoliths were extracted for age interpretation and were washed and stored dry prior to sectioning. One otolith was randomly selected and embedded in epoxy resin. A transverse section (~300 nm thick) was made perpendicular to the sulcus acusticus with a double-bladed low-speed isomet saw. The section was mounted on a microscope slide and photographed using an Olympus SZX16 stereoscope with transmitted light and an Olympus QColor5<sup>®</sup> digital camera. Otolith sections were examined by two independent 'agers' for annulus characteristics, such as changes in circuli spacing and cutting over, prior to counting and measuring annuli.

## Data analysis

We examined differences in length, weight and age among cisco species using one-way analysis of variance. Data were combined across sample years and geographic areas. When significant differences were detected, Tukey HSD tests were performed to separate groups. Among-species differences in sex ratios were assessed using a log-linear analysis (Zar, 1999). Differences in mean age among sexes were assessed using a two-sample t-test.

Mortality, survival and von Bertalanffy analyses were computed with R Version 2.10.1 (R Development Core Team, 2009), using the Fisheries Stock Assessment program (FSA-package) developed by Dr. Derek Ogle at Northland College, Wisconsin. Ages were determined from a large sub-sample (2251 fish were aged) of the overall catch from all three years combined. An age-length key was used to assign ages to individual un-aged fish using the methods described by Isermann and Knight (2005). Mortality estimates were calculated from the descending limb of the catch curve for each species. The von Bertalanffy growth function (1) was fit to the age-length data for each species:

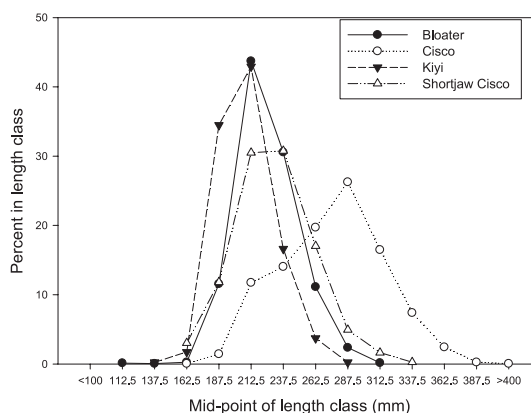
$$L(t) = L_{\infty}[1 - e^{-k(t-t_0)}] \quad (1)$$

For our analyses we used fork lengths (FL). Three common length measures were used in earlier publications on deepwater ciscoes: standard length (SL), FL, and total length (TL). For example, Koelz (1929) reported lengths of all ciscoes as SL. To ensure valid comparisons with published data, we measured lengths in 1883 ciscoes using all three common length measures. The three measures were nearly perfectly correlated across all species (all  $r$ 's > 0.99), and the resulting conversions were (1) SL = 0.9483 FL, (2) SL = 0.8677 TL and (3) FL = 0.9146 TL. These conversions allow our reported lengths (FL) to be converted to SL or TL or vice versa.

## Results

Over 6000 ciscoes were netted during the three sampling years (Table 1). Bloaters ( $n = 3711$ ) were the most commonly observed species, followed by Cisco ( $n = 1497$ ). The two species of conservation concern, Kiyi ( $n = 420$ ) and Shortjaw Cisco ( $n = 388$ ), were least commonly captured. Western management units contained particularly high densities of Bloater and Cisco relative to northern and eastern areas, while Kiyi and Shortjaw Cisco were more evenly distributed across the sampling areas (Table 1).

Cisco are the largest species in the Lake Superior Deepwater Cisco fauna, followed by Shortjaw Cisco, Bloater and Kiyi (Figure 2; Table 2;  $F_{3,5727} = 1284.2$ ,  $P < 0.001$ ; Tukey HSD,  $P < 0.001$  in all comparisons). Cisco also had the broadest size



**Figure 2.** Deepwater Cisco size distribution, by fork length intervals (mm), from experimental gill nets set in the Canadian waters of Lake Superior. The mid-point of each length class is presented on the x-axis (e.g. the 100–124.9 mm length class is represented by 112.5 mm).

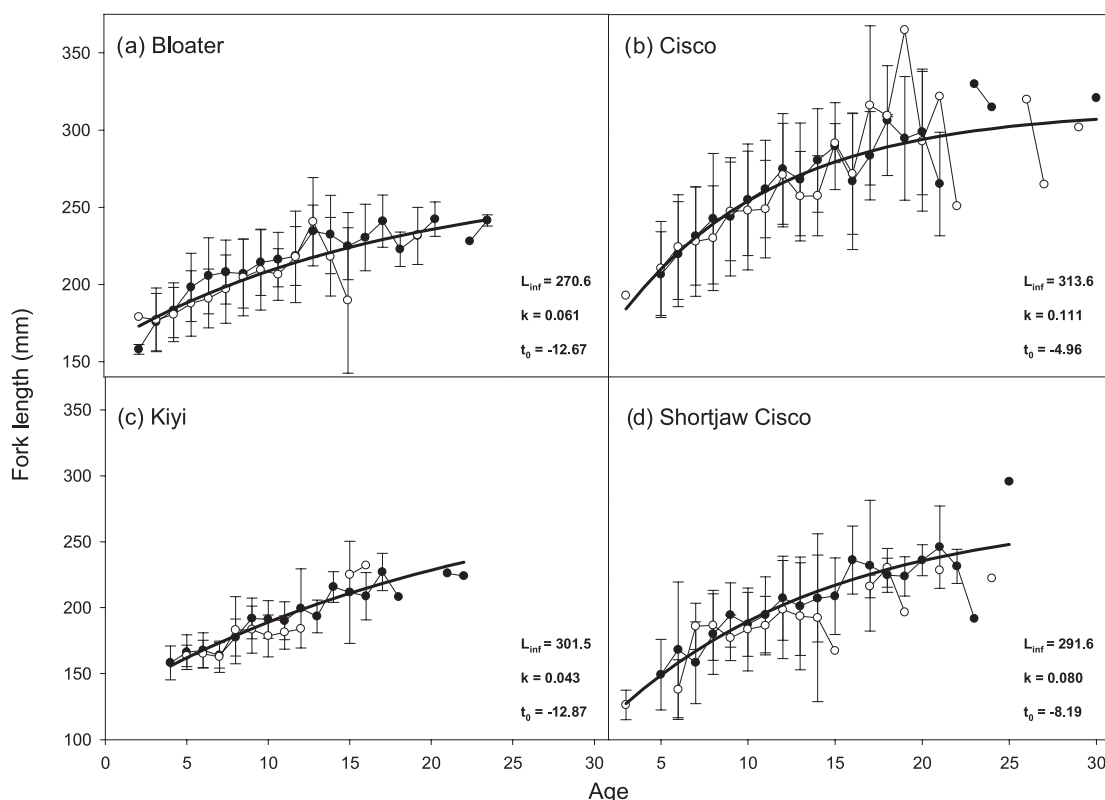


range, while Kiyi had a narrow size range (Figure 2). Significant differences in mean weight were also observed ( $F_{3,6015} = 1148.5$ ,  $P < 0.001$ ), with Cisco as the heaviest species and Kiyi the lightest (Table 2; Tukey HSD,  $P < 0.001$  in all comparisons). Significant differences in the mean age of deepwater ciscoes were also detected ( $F_{3,2247} = 27.5$ ,  $P < 0.001$ ). Among the Cisco, mean age of Shortjaw Cisco was the oldest and that of Kiyi the youngest. Cisco and Bloater mean ages were different than the other two species, but not different from each other (Table 2; Tukey HSD,  $P = 0.80$  for Cisco and Bloater,  $P < 0.001$  in all remaining comparisons). All four species had similar age ranges, though Cisco had the largest range from 3–30 years (Table 2, Figure 3). Species-specific von Bertalanffy growth curves for the most part corroborated the among-species differences, as Cisco had the highest growth coefficient, followed by Shortjaw Cisco, Bloater and Kiyi (Figure 3). The only apparent anomaly was the large

asymptotic FL (301.5 mm) of Kiyi, as no specimens that large were collected in our sampling.

Females dominated sex ratios for all four species, though the proportion of females did vary significantly among species (Table 2; Maximum likelihood  $\chi^2 = 79.2$ ,  $P < 0.001$ ). Kiyi had the most skewed sex ratio, with nearly 77% females, followed closely by Bloater with 75% female. Cisco had the most balanced sex ratio, with 59% of the fish identified as female (Table 2). It was apparent that our gill nets were not able to effectively sample younger, immature fish, as nearly all fish assessed were sexually mature (Table 2).

Among-sex variability in age and growth was apparent in all four cisco species. Females were older and larger than males, though the magnitude of these differences varied among species (Table 2; Figure 3). Mean female age was significantly older in Bloater, Cisco, and Shortjaw Cisco (Table 2; Bloater  $t_{898} = 777$ ,  $P < 0.001$ ; Cisco  $t_{720} = 2.21$ ,



**Figure 3.** Mean size-at-age, by sex, for Lake Superior deepwater ciscoes. Male data are represented with open circles, while female data are represented with closed circles. The lines represent sexes combined fitted von Bertalanffy growth curves, and curve parameters, including asymptotic length ( $L_{inf}$ ), growth coefficient ( $k$ ), and initial fork length ( $t_0$ ) are in the lower right hand corner of each plot.

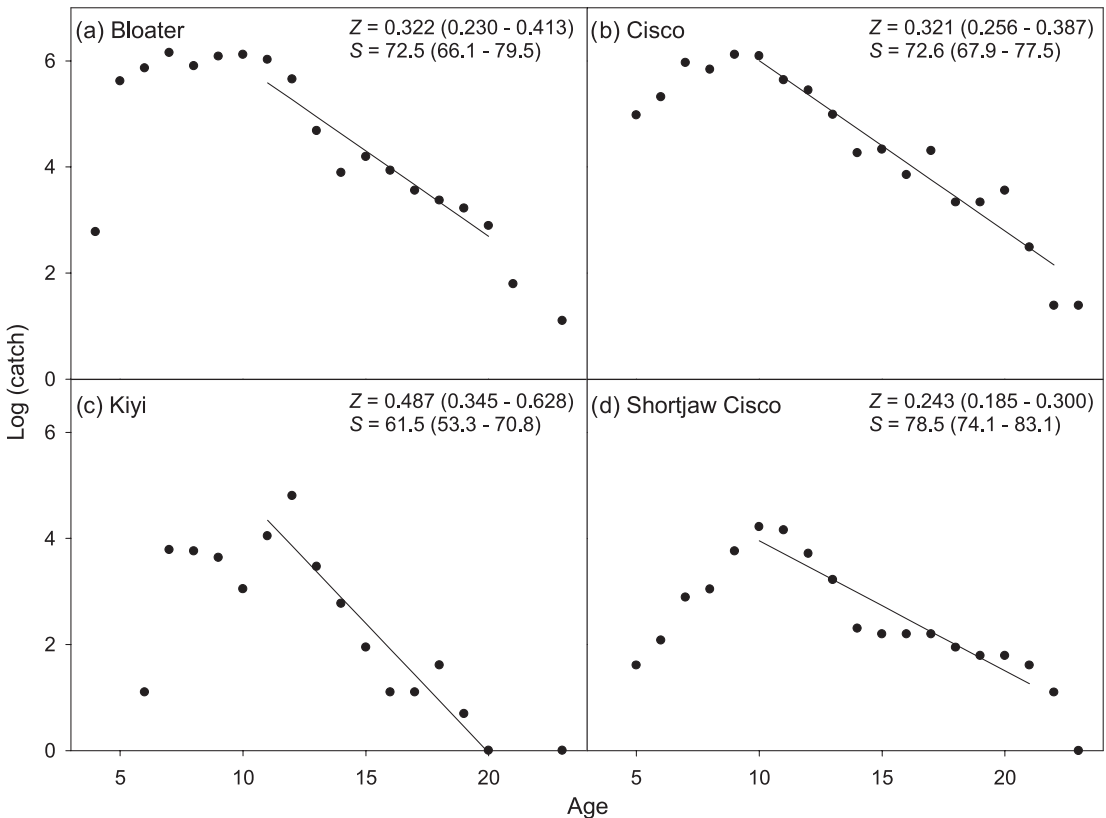
$P = 0.027$ ; Shortjaw Cisco  $t_{300} = 2.46$ ,  $P = 0.014$ ), but not Kiyi ( $t_{320} = 1.79$ ,  $P = 0.075$ ). Females were slightly larger than males over the majority of ages for all four species, and had greater longevity than males except in Cisco (Figure 3).

Estimates of total annual survival were generally high for the four Lake Superior cisco species (Figure 4). Kiyi had the lowest rate of annual survival at 61.5%, while Shortjaw Cisco had the highest at 78.5%.

# Discussion

Our findings provide an important update of the life history characteristics of deepwater ciscoes in Lake Superior, particularly for Bloater, Kiyi and Shortjaw Cisco. Cisco, typically considered a shallow-water form, was found in relatively high abundance in our deepwater sets and is currently an important component of the Deepwater Cisco community (Pratt, 2012), so we included it in our assessment. While researchers have recently addressed

the ecology of deepwater ciscoes in Lake Superior (Hrabik et al., 2006; Jensen et al., 2006; Gorman and Todd, 2007; Schmidt et al., 2009; Stockwell et al., 2010; Gorman, 2012), and the biology and life history of Bloater in other Great Lakes (Bunnell et al., 2006; Bunnell et al., 2009; Bunnell et al., 2010), with the exception of Cisco (Yule et al., 2008; Stockwell et al., 2009), very little or no recent biological information exists on the life history characteristics of Lake Superior's ciscoes. The most recent comprehensive examinations of Bloater (Dryer and Beil, 1968), Kiyi (Koelz, 1929), and Shortjaw Cisco (Van Oosten, 1937) from Lake Superior are many decades old. The majority of our results are not surprising, as they reflect what has been found previously for ciscoes in other Great Lakes or historical data from Lake Superior, but we believe that confirmation of these characteristics in Lake Superior ciscoes is still important, especially for species of conservation concern such as Kiyi and Shortjaw Cisco. Our key finding was that these fishes have greater longevity than previously reported. Consequently, survival



**Figure 4.** Rates of total annual survival ( $S$ ) and instantaneous mortality ( $Z$ ) for deepwater ciscoes captured in Lake Superior. Numbers in brackets represent 95% confidence intervals.

estimates were higher than previous estimates that used scale age interpretations. We found considerable overlap but significant differences in the growth and age distributions of the four cisco species, and differences in size and age between sexes within species. Sex ratios were highly skewed towards females, which were generally larger at-age and demonstrated greater longevity than males. Each of our principal conclusions, along with a comparison of the life history information for Lake Superior's ciscoes, is discussed below.

## Survival and mortality

Fisheries managers have relied on scales to interpret fish age for many decades, despite increasing evidence that scales underestimate age, particularly in longer-lived fishes including coregonids (Mills and Beamish, 1980; Barnes and Power, 1984; Coffin et al., 2003; Howland et al., 2004; Yule et al., 2008). One consequence of using ages derived from scales to estimate survival and mortality in older fish is that survival is underestimated; this was clearly demonstrated in Cisco from Lake Superior by Yule et al (2008), who found otolith-derived estimates of survival of 0.75–0.80, while earlier scale-derived estimates ranged from 0.25–0.42 (Segelby, 1982; Bowen et al., 1991). Our annual survival estimate of 0.73 for Cisco is similar to the Yule et al. (2008) estimates. There are no published otolith-derived estimates of survival for Bloater, Kiyi or Shortjaw Cisco against which we can compare our findings. The catch-curve approach that we used to determine survival is based on three assumptions: that (1) the population is sampled randomly, (2) the survival rate is uniform with age and there is no change with time and (3) there is constant and steady recruitment into the population (Ricker, 1975). We addressed the first assumption as best we could by use of a gear capable of catching a wide age range, and combining samples across years and locations. Given that we have no comparable survival data for these fishes with the exception of the Yule et al. (2008) estimate for Cisco, it is not possible to determine whether the second assumption was violated, except to note that this assumption is primarily a concern when fishing mortality is present (Ricker, 1975), and there is almost no current fishery for ciscoes in Lake Superior with the exception of a fall Cisco fishery. The third assumption is potentially more troublesome, as recruitment in Lake Superior ciscoes is clearly episodic (Bronte et al., 2003; Gorman and Hoff,

2009). However, Allen (1997) demonstrated that estimates of survival are generally quite robust ( $\pm 10\%$ ) even with high recruitment variation. Given the paucity of data available for these species and the relative robustness of the analysis to violation of these assumptions, we believe that our results are likely reasonable and valuable as a starting point for fishery managers interested in assessing the status of present and future populations of ciscoes.

The range of annual survival estimates among the four cisco species may be partly explained by their growth and age patterns. Piscivores are gape-limited, meaning that smaller fish are vulnerable to a greater number of predators (Hambright, 1991). Kiyi, the smallest and shortest-lived Cisco in our survey, had the highest annual mortality estimate of the four ciscoes that we examined, possibly due to higher predation mortality on this species. Our understanding of Kiyi ecology has advanced considerably in the past decade; they undergo extensive daily vertical migrations following their main prey, *Mysis relicta*, and in turn are followed by their primary predator, siscowet Lake Trout (*Salvelinus namaycush siscowet*) (Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010; Gorman et al., 2012). Bloater, which is also relatively small, had a similar mortality estimate as Cisco, which is the largest Cisco species in Lake Superior. This might suggest that size-specific predation is not the mechanism for differential mortality among cisco species, except that Cisco is subject to a commercial fishery and a fishing mortality rate of up to 9% annually (Yule et al., 2008), which the deepwater ciscoes are not subject to. Without this mortality factor, Cisco would have similar annual mortality estimates to Shortjaw Cisco, the second-largest and longest-lived cisco species in Lake Superior.

## Age, growth and sex ratio

Previously published accounts on the age and growth of ciscoes are likely inaccurate, with the exception of the youngest ages, given that early accounts were based on scale age interpretation. That said, our observations of differences between males and females in size-at-age and longevity have been observed in Great Lakes ciscoes for many decades even with the lower resolution allowed for by scale age interpretation. Higher female longevity has been noted in all Great Lakes deepwater ciscoes (Van Oosten, 1937; Deason and Hile, 1947; Dryer and Beil, 1964; Dryer and Beil, 1968), likely



because of differential mortality among the sexes. Male Bloater have higher natural mortality in Lake Michigan (TeWinkel et al., 2002), and male Cisco have higher natural mortality in Lake Superior (Yule et al., 2008). The most common hypotheses for differential mortality include sex-specific differences in age-at-maturity, and/or mortality due to predation or competition for scarce resources (Britton and Moser, 1982; Clutton-Brock, 1986; Girondot and Pieau, 1993). Nearly all the ciscoes examined in this study were already mature, so we were unable to assess for differences in sex-specific maturity schedules. Given that females achieved larger size-at-age than males at ages for which we had good sample sizes for all species, and predators in Lake Superior are gape-limited, it is likely that males are more vulnerable to predation than females. This contention is supported by the diet data of lean (*S. namaycush namaycush*) and siscowet Lake Trout predators in Lake Superior, which demonstrates that smaller ciscoes are more vulnerable to a large, restored predator base (Conner et al., 1993; Mason et al., 1998; Ray et al., 2007).

Cisco was the largest and fastest growing of this species in Lake Superior, with an estimated growth coefficient that was double that of Kiyi and Bloater. The faster growth may be explained by habitat or diet differences, as Cisco captured in shallow water consume more zooplankton and have a more diverse diet than deepwater ciscoes (Anderson and Smith, 1971). However, there is no diet data available for Cisco captured at deeper depths, like those in our study. Our use of the traditional von Bertalanffy analyses with only adult fish may have resulted in the overestimation of asymptotic lengths; there is an increasing body of literature that recommends the use of growth models that incorporate a separate pre- and post-maturation component (Day and Taylor, 1997; Lester et al., 2004). Nonetheless, we believe that our growth data are illustrative for comparison purposes.

There appears to have been very little change in the size structure of deepwater ciscoes over the past century in Lake Superior, in contrast to what has been observed in the lower Great Lakes. Bloater size has varied over time in Lake Superior; mean size increased 30 mm over a relatively short 8 year time period in experimental (25–127 mm) gill nets (Dryer and Beil, 1968). However, the mean size in our study is within 5 mm of the earlier part of the Dryer and Beil (1968) sampling period. Similarly, our mean size of Shortjaw Cisco was within 10 mm of the

previously published mean lengths for the species in Lake Superior (Van Oosten, 1937; Hoff and Todd, 2004). Koelz (1929) noted that Kiyi from Lake Superior were smaller than from the other Great Lakes, with a FL range of 139–215 mm (converted from Koelz's SL). Our data indicates that while Kiyi may grow a little larger than they did in the 1920s, they remain the smallest Cisco in the lake, and Kiyi in Lake Superior are significantly smaller than they were historically in Lake Michigan, where the mean FL of 281 mm was larger than our largest specimen (Deason and Hile, 1947).

In our survey, females dominated the adult populations in all four species, with Cisco having the most balanced (59% female) and Kiyi (77% female) having the least balanced sex ratios. Sex ratio is an important reflection of recruitment patterns in ciscoes (Bunnell et al., 2006), with more balanced sex ratios signifying recent strong recruitment events. We do not know the sex ratios of immature ciscoes as immature fish were not vulnerable to our gear. Dryer and Beil (1968) noted that nearly all Lake Superior Bloater were mature by age 3, which may explain why we rarely captured immature fish as they didn't recruit to our gill nets until age 4. Adult sex ratios in ciscoes can vary widely; the best example of this is from Lake Michigan, where the percentage of female bloaters has ranged from 36% to 97% over the past century (Jobes, 1949; Bunnell et al., 2006). Though data are scarcer, there is evidence that sex ratios have also changed over time in Lake Superior. The sex ratio of Cisco has been as high as 75% female (Bowen et al., 1991), at a time when population levels were depressed; our observation of ~60% female in the current population is similar to many of the populations assessed by Dryer and Beil (1964), and it is likely indicative of recent recruitment events in the Lake Superior Cisco population (Stockwell et al., 2009). In contrast, the Shortjaw Cisco sex ratio has become increasingly skewed over the years, ranging from a low of 55% female in the earliest sampling period (Van Oosten, 1937) to ~70% female in our assessment. This phenomenon is found in many cisco populations, and there are a number of explanations for differential survival of the sexes including increased mortality due to predation or vulnerability to a fishery, differences growth rate and an associated survival trade-off, or differences in reproductive activity or maturation schedule (Bunnell et al., 2006). The high female dominance observed in our survey for the deepwater ciscoes likely indicates that recruitment

for these species in Lake Superior has been poor over the past couple of decades.

## Conclusions

Deepwater ciscoes remain an important but poorly studied component of the offshore community in Lake Superior, the only Great Lake that has maintained its historic Cisco complement. A current understanding of the life history characteristics of ciscoes in Lake Superior is important given the conservation concerns about the Deepwater Cisco flock in the Great Lakes, and the interest in re-establishing deepwater ciscoes in lakes where they have been extirpated. Our work confirms that deepwater ciscoes, like Cisco, are long-lived, and likely do not have high intrinsic rates of recovery (Yule et al., 2008). However, it should be noted that large Cisco year-classes have been produced from low stock sizes (Bronte et al., 2003; Gorman and Hoff, 2009). Many of the life history characteristics examined in our study have not changed since the early part of the 20<sup>th</sup> century, prior to the radical changes observed in Cisco community composition (Bronte et al., 2010; Gorman, 2012; Pratt, 2012).

## Acknowledgements

Our work was funded by the Canada-Ontario Agreement Respecting the Great Lakes Basin Ecosystem (COA) and DFO Species at Risk Program (SARCEP). We thank Lisa O'Connor, Bill Gardner, John Deeg, Jon Chicoine, Dave Montgomery, Cheryl Widdifield, Grant Fortin, Janice McKee and Kim Caldwell for all their efforts in the field and in the laboratory. Owen Gorman and two anonymous reviewers provided helpful criticisms of an earlier draft of the article.

## References

- Allen, M.S., 1997. Effects of variable recruitment on catch-curve analysis for Crappie populations. *North Am. J. Fish. Manage.* 17, 202–205.
- Anderson, E.D., Smith, L.L., Jr., 1971. A synoptic study of food habits of 30 fish species from western Lake Superior. *Univ. Minn. Agri. Exp. Station Tech. Bull.* 279.
- Barnes, M.A., Power, G., 1984. A comparison of otolith and scale ages for western Labrador Lake Whitefish, *Coregonus clupeaformis*. *Environ. Biol. Fishes* 10, 297–299.
- Bowen, S.H., D'Angelo, D.J., Arnold, S.H., Keniry, M.J., Albrecht, R.J., 1991. Density-dependent maturation, growth, and female dominance in Lake Superior Lake Herring (*Coregonus artedii*). *Can. J. Fish. Aquat. Sci.* 48, 569–576.
- Britton, R.H., Moser, M.E., 1982. Size specific predation by herons and its effect on the sex-ratio of natural populations of the Mosquito Fish *Gambusia affinis* Baird and Girard. *Oecologia* 53, 146–151.
- Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., Lozano, S.J., 2003. Fish community changes in Lake Superior, 1970–2000. *Can. J. Fish. Aquat. Sci.* 60, 1552–1574.
- Bronte, C.R., Hoff, M.H., Gorman, O.T., Thogmartin, W.E., Schneeberger, P.J., Todd, T.N., 2010. Decline of the Shortjaw Cisco in Lake Superior: The role of overfishing and risk of extinction. *Trans. Am. Fish. Soc.* 139, 735–748.
- Bunnell, D.B., Madenjian, C.P., Croley III, T.E., 2006. Long-term trends in Bloater recruitment in Lake Michigan: evidence for the effect of sex ratio. *Can. J. Fish. Aquat. Sci.* 63, 832–844.
- Bunnell, D.B., David, S.R., Madenjian, C.P., 2009. Decline in Bloater fecundity in southern Lake Michigan after decline of *Diporeia*. *J. Great Lakes Res.* 35, 45–49.
- Bunnell, D.B., Adams, J.V., Gorman, O.T., Madenjian, C.P., Riley, S.C., Roseman, E.F., Schaeffer, J.S., 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effects of dispersal and climate. *Oecologia* 162, 641–651.
- Clutton-Brock, T.H., 1986. Sex ratio variation in birds. *Ibis* 128, 317–329.
- Coffin, A.B., Pereira, D.L., Spangler, G.R., 2003. Stock specific growth rates of Lake Herring, *Coregonus artedii*, in western Lake Superior. *Environ. Biol. Fishes* 68, 39–48.
- Conner, D.J., Bronte, C.R., Selgeby, J.H., Collins, H.L., 1993. Food of salmonine predators in Lake Superior, 1981–1987. *Great Lakes Fish. Comm. Tech. Rep.* 59, Ann Arbor, Michigan, USA.
- Day, T., Taylor, P.D., 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.* 149, 381–393.
- Deason, H.J., Hile, R., 1947. Age and growth of the Kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. *Trans. Am. Fish. Soc.* 74, 553–572.
- Dryer, W.R., Beil, S., 1964. Life history of Lake Herring in Lake Superior. *Fish. Bull.* 63, 493–530.
- Dryer, W.R., Beil, S., 1968. Growth changes of the Bloater (*Coregonus hoyi*) of the Apostle Islands region of Lake Superior. *Trans. Am. Fish. Soc.* 97, 146–158.
- Favé, M.J., Turgeon, J., 2008. Patterns of genetic diversity in Great Lakes bloaters (*Coregonus hoyi*) with a view to future reintroduction in Lake Ontario. *Conserv. Genet.* 9, 281–293.
- Girondot, M., Pieau, C., 1993. Effects of sexual differences of age at maturity and survival on population sex ratio. *Evol. Ecol.* 7, 645–650.
- Gorman, O.T., 2012. Successional change in the Lake Superior Fish community: Population trends in ciscoes, Rainbow Smelt, and Lake Trout, 1958–2008. In: K. H. Mills, R. F. Tallman, K. L. Howland, M. D. Rennie (Eds.), *Biology and Management of Coregonid Fishes 2008*. *Adv. Limnol.* 63, 337–362.
- Gorman, O.T., Todd, T.N., 2007. History of the Shortjaw Cisco (*Coregonus zenithicus*) in Lake Superior, 1895–2003. *Adv. Limnol.* 60, 433–458.
- Gorman, O.T., Hoff, M.H., 2009. Changes in the Lake Superior fish community during 1978–2003: Chronicling the recovery

- of a native fauna. In: M. Munawar and I.F. Munawar (Eds.), *State of Lake Superior*, pp. 493–532. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Burlington, Ontario.
- Gorman, O.T., Yule, D.L., Stockwell, J.D., 2012. Habitat uses by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Island region. *Aquatic Ecosystem Health and Management* 15(3), 333–354.
- Hambright, K.D., 1991. Experimental analysis of prey selection by Largemouth Bass: role of predator mouth width and prey body depth. *Trans. Am. Fish. Soc.* 120, 500–508.
- Hoff, M.H., Todd, T.N., 2004. Status of the Shortjaw Cisco (*Coregonus zenithicus*) in Lake Superior. *Ann. Zool. Fennici* 41, 147–154.
- Howland, K.L., Gendron, M., Tonn, W.M., Tallman, R.F., 2004. Age determination of a long-lived coregonid from the Canadian North: comparison of otoliths, fin rays and scales in inconnu (*Stenodus leucichthys*). *Ann. Zool. Fennici* 41, 205–214.
- Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J., Kitchell, J.F., 2006. Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. *Can. J. Fish. Aquat. Sci.* 63, 2286–2295.
- Isermann, D.A., Knight, C.T., 2005. A computer program for age-length keys incorporating age assignment to individual fish. *North Am. J. Fish. Manage.* 25, 1153–1160.
- Jensen, O.P., Hrabik, T.R., Martell, S.J.D., Walters, C.J., Kitchell, J.F., 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. *Can. J. Fish. Aquat. Sci.* 63, 2296–2307.
- Jobes, F.W., 1949. The age, growth, and bathymetric distribution of the Bloater, *Leucichthys hoyi* (Gill) in Lake Michigan. *Pap. Mich. Acad. Sci., Arts Lett.* 33, 135–172.
- Koelz, W., 1929. Coregonid fishes of the Great Lakes. *Bull. U.S. Bur. Fish.* 43, 297–643.
- Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *P. Roy. Soc. Lond. B Bio.* 271, 1625–1631.
- Mason, D.M., Johnson, T.B., Kitchell, J.F., 1998. Consequences of prey fish community dynamics on Lake Trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. *Can. J. Fish. Aquat. Sci.* 55, 1273–1284.
- Mills, K.H., Beamish, R.J., 1980. Comparison of fin-ray and scale age determinations for Lake Whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. *Can. J. Fish. Aquat. Sci.* 37, 534–544.
- Pratt, T.C., 2012. The distribution and abundance of deepwater ciscoes in Canadian waters of Lake Superior. In: R.F. Tallman, K.L. Howland, M.D. Rennie, K.H. Mills (Eds.), *Biology and Management of Coregonid Fishes 2008*. *Adv. Limnol.* 63, 25–41.
- R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.r-project.org>.
- Ray, B.A., Hrabik, T.R., Ebener, M.P., Gorman, O.T., Schreiner, D.R., Schram, S.T., Sitar, S.P., Mattes, W.P., Bronte, C.R., 2007. Diet and prey selection by Lake Superior Lake Trout during spring, 1986–2001. *J. Great Lakes Res.* 33, 104–113.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can. Bull.* 191.
- Schmidt, S.N., Vander Zanden, M.J., Kitchell, J.F., 2009. Long-term food web change in Lake Superior. *Can. J. Fish. Aquat. Sci.* 66, 2118–2129.
- Smith, S.H., 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. *J. Fish. Res. Bd. Can.* 29, 717–730.
- Stockwell, J.D., Ebener, M.P., Black, J.A., Gorman, O.T., Hrabik, T.R., Kinnunen, R.E., Mattes, W.P., Oyadomari, J.K., Schram, S.T., Schreiner, D.R., Seider, M.J., Sitar, S.P., Yule, D.L., 2009. A synthesis of Cisco recovery in Lake Superior: implications for native fish rehabilitation in the Laurentian Great Lakes. *North Am. J. Fish. Manage.* 29, 626–652.
- Stockwell, J.D., Hrabik, T.R., Jensen, O.P., Yule, D.L., Balge, M., 2010. Empirical evaluation of predator-driven diel vertical migration in Lake Superior. *Can. J. Fish. Aquat. Sci.* 67, 473–485.
- TeWinkel, L.M., Kroeff, T., Fleischer, G.W., Toney, M., 2002. Population dynamics of Bloater (*Coregonus hoyi*) in Lake Michigan, 1973–1998. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 57, 307–320.
- Todd, T.N., Smith, G.R., 1992. A review of differentiation in Great Lakes ciscoes. *Pol. Arch. Hydrobiol.* 39, 261–267.
- Van Oosten, J., 1937. The age, growth, and sex ratio of the Lake Superior Longjaw, *Leucichthys zenithicus* (Jordan and Evermann). *Pap. Mich. Acad. Sci. Arts, Letters* 22, 691–711.
- Yule, D.L., Stockwell, J.D., Black, J.A., Cullis, K.I., Cholewek, G.A., Myers, J.T., 2008. How systematic age underestimation can impede understanding of fish population dynamics: lessons learned from a Lake Superior Cisco stock. *Trans. Am. Fish. Soc.* 137, 481–495.
- Zar, J.H., 1999. *Biostatistical Analysis*, 4th Edn. Prentice-Hall, Englewood Cliffs, N.J.
- Zimmerman, M.S., Krueger, C.C., 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. *North Am. J. Fish. Manage.* 29, 1352–1371.

Copyright of Aquatic Ecosystem Health & Management is the property of Taylor & Francis Ltd and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.